Available online at www.sciencedirect.com

SCIENCE DIRECT®

Vision Research 45 (2005) 707–714

Vision Research

www.elsevier.com/locate/visres

# Mechanisms selectively engaged in rivalry: normal vision habituates, rivalrous vision primes

Joel Pearson *, Colin W.G. Clifford

*Colour, Form and Motion Lab, Visual Perception Unit, School of Psychology, The University of Sydney, NSW 2006, Australia*

Received 22 July 2004; received in revised form 24 September 2004

**Abstract**

When rivalrous stimuli are presented intermittently, perception stabilises. This indicates the operation of perceptual memory across interruptions in stimulation. Here we show that a percept under non-rivalrous and rivalrous conditions has qualitatively different effects on subsequent rivalrous vision. When an image is perceived under rivalrous viewing, that image is more likely to be perceived in later rivalrous viewing: an effect of stabilisation or priming. When the same image is perceived under non-rivalrous viewing conditions, it is less likely to be perceived again during subsequent rivalrous viewing: an effect of adaptation or habituation. When these stimuli possess different attributes to those in subsequent vision their effect declines. This suggests that visual rivalry might recruit mechanisms that are not engaged in 'normal' non-rivalrous vision but perhaps dedicated to the resolution of competing sensory information.



*Keywords:* Visual awareness; Binocular rivalry; Stimulus rivalry; Memory; Priming; Neural fatigue; Neural competition

## 1. Introduction

Visual competition provides an incisive tool to study the neural correlates of visual awareness (Blake & Logothetis, 2002; Crick & Koch, 1998; Engel, Fries, Konig, Brecht, & Singer, 1999; Logothetis, 1998, 1999). A binocular rivalry (BR: Wheatstone, 1838) stimulus consists of different images presented to corresponding regions of the two eyes. Rivalry is also experienced using a different type of presentation, stimulus rivalry (SR; Logothetis, Leopold, & Sheinberg, 1996), in which the images presented to the eyes are swapped every ~300 ms. During both these types of rivalry observers experience salient alternations in visual awareness, one image dominates while the other is suppressed. During BR, stimulation at low levels of the visual system remains constant. During SR, each period of perceptual dominance typically spans across several eye-swaps. Thus, in both forms of rivalry, low-level stimulation is uncorrelated with the spontaneous alternations in visual awareness experienced by observers, providing a dissociation between visual stimulation and visual awareness.

If patterns undergoing BR and SR are made to disappear from awareness for a short period, the stimulus in awareness as they disappear tends to be the one perceived when they reappear (Chen & He, 2004; Leopold, Wilke, Maier, & Logothetis, 2002; Pearson & Clifford, 2004; Ross & Ma-Wyatt, 2004). This stability during intermittent rivalry indicates the operation of some kind of perceptual memory across interruptions in stimulation. The content of this memory has been found to depend on the type of rivalry. During BR it is dominated by eye-of-origin information, while during SR it contains primarily colour information (Chen & He, 2004; Pearson & Clifford, 2004).

In the current study we investigated the vulnerability of short-term perceptual memory during intermittent BR and SR to visual interruptions consisting of BR,

* Corresponding author. Tel.: +61 293517636; fax: +61 293512603.
*E-mail address:* joelp@psych.usyd.edu.au (J. Pearson).

0042-6989/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2004.09.040

SR and different *non-rivalrous* presentations. We present evidence that non-rivalrous and rivalrous vision have qualitatively different effects on subsequent rivalrous vision. This finding complements research that has documented brain areas selectively engaged in competitive vision (Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Lumer & Rees, 1999; Lumer, Friston, & Rees, 1998; Meenan & Miller, 1994; Ricci & Blundo, 1990).

## 2. Methods

### 2.1. Subjects

The same four subjects (2 male, 2 female) participated in all conditions of all experiments. All subjects had normal vision. The two authors served as subjects. The other subjects were experienced psychophysical observers who were naive to the purpose of the study. All observers gave informed written consent before participating in the experiment.

### 2.2. Stimuli

Stimuli were sinusoidal gratings generated using Matlab software to drive a VSG 2/5 Graphics Card (Cambridge Research Systems), displayed on a gamma-corrected 21″ Sony Trinitron GM 520 monitor ($1024 \times 768$ resolution; 120 Hz refresh rate), and viewed through a mirror stereoscope adjusted for each observer, one grating presented to each eye. Each grating had a spatial frequency of 0.93 cyc/°, an orientation of ±45° (unless otherwise stated), and was presented in a 4.2° diameter circular aperture. The contrast of each grating was 30%, with an average luminance equal to that of the background (6 $Cd\,m^{-2}$). A bullseye fixation spot was used to aid in convergence. One grating was green while the other was always red, unless otherwise stated. The colour coordinates of red were (CIE: $x = 0.63$; $y = 0.34$), green (CIE: $x = 0.28$; $y = 0.62$), yellow (CIE: $x = 0.46$; $y = 0.48$) and purple (CIE: $x = 0.28$; $y = 0.25$); the luminance of the yellow/purple gratings was the same as that for the red/green gratings. The background colour was an average of all the colours used in that condition. To obtain SR, gratings swapped between the eyes 4 times a second (2 Hz). Stimuli were oscillating on/off at 20 Hz in all experiments to equate the BR trials with the SR trials, as on/off oscillations are required for SR (Lee & Blake, 1999; Logothetis et al., 1996).

### 2.3. Procedure

Subjects used a chin rest to view all displays and were instructed to fixate the bullseye fixation spot. On different blocks of 40 trials the task was to signal either the colour or orientation of the dominant grating during the test rivalry display. This was done to balance any effect of attention on our results. There were no significant differences in the data from trials in which subjects signalled orientation and colour (not shown). Audible beeps denoted the time for an observer to respond, this was to ensure that subjects did not change their response times as this may have affected perceptual stability. Subjects signalled the percept by pushing one of two response buttons. The responses were then recorded by a computer and analysed offline. Observers were instructed to respond to the dominant grating during the test rivalry. If a percept was mixed or piecemeal, they were required to make a forced-choice decision. The general time line for all experiments is illustrated in Fig. 1a.

## 3. Results

In our first experiment we investigated how this perceptual memory is disrupted by *rivalrous* percepts. Perpendicular red and green gratings were used as rivalrous stimuli (see Section 2). The 'test' gratings were presented for 750 ms, followed by a 3 s gap in presentation (see Fig. 1a). Under these conditions rivalry is stabilised (BR: Leopold et al., 2002; BR & SR: Pearson & Clifford, 2004). For the middle second of that gap different rivalrous gratings were presented to subjects. To control the dominant percept during the interrupting stimulus we utilised a technique called flash suppression (Wolfe, 1984; Wilke, Logothetis, & Leopold, 2003; see Fig. 1b: BR, c: SR) in which two stimuli are presented asynchronously to an observer. As the second image is presented rivalry is induced and perception switches to it, even though the initial image is continually displayed. This allowed us to control the dominant grating during the interrupting rivalry. We will refer to the 'same' grating or percept, meaning the same grating in the latter half of flash suppression (or mock) as that dominant during the previous test phase of rivalry. For the BR conditions this includes the *same eye* as well as the same grating, the 'opposite' grating or percept refers to the grating/eye opposite to that previously dominant during the test rivalry.

The results from the first experiment (Fig. 2a and b) demonstrate that when the *opposite* percept (opposite to that which a subject had previously signalled) was 'forced' as an interruption subjects perceptual stability was *reduced*, for BR to below the chance level of 50% and for SR to around chance (Fig. 2a and b; right columns). However, when the 'same' percept (that which a subject had previously signalled) was dominant during the interrupting rivalry, perceptual stability remained high (Fig. 2a and b; left columns). A repeated-measurements ANOVA shows that the effect of the percept (same or opposite) was highly significant for BR–BR

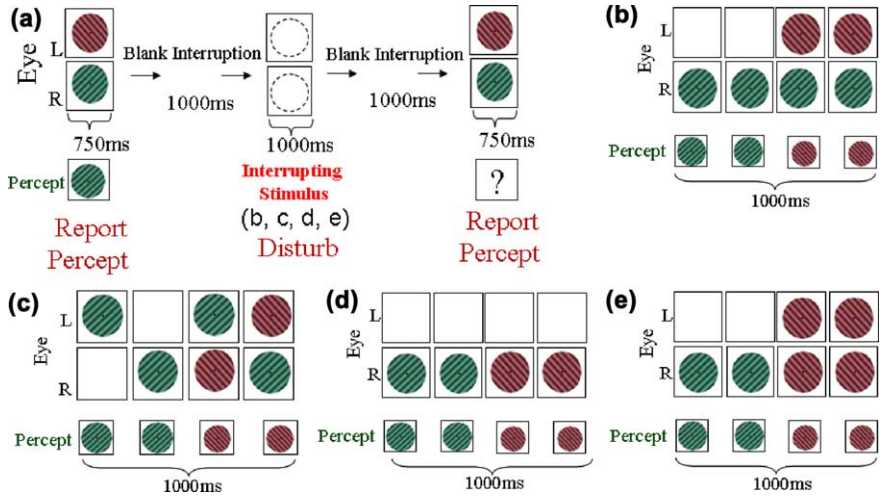


Fig. 1. Graphical display of the timeline of all experiments and the stimuli used as interruptions. (a) Time is represented along the *x*-axis, eyes on the *y*. The upper panel illustrates the physical stimuli, the lower panel illustrates the percept before the interruption and the question mark represents whether or not the test rivalry is stable. The central column represents the presentation of the different disturbing stimuli for all experiments. Here the interrupting stimuli utilised flash suppression whereas the test stimuli did not. (b) The BR interruption, utilising flash suppression. As the red grating appears perception typically switches to it. (c) The SR interruption, also utilising a stimulus rivalry version of flash suppression. Perceptually the sequence was the same for all the interrupting stimuli. (d) The non-rivalrous interruption stimuli used to disrupt BR, with simulated flash suppression. (e) The non-rivalrous interruption stimuli used to disrupt SR. During the later 500 ms the same grating is displayed to both eyes. (For interpretation of the references in colour in this figure, the reader is referred to the web version of this article.)

($P = 0.001$) and SR–SR ($P = 0.007$), while the effect of subjects was not significant (BR: $P = 0.48$; SR: $P = 0.11$). Another way to conceptualize these results is that when the interrupting percept is 'forced' to be the opposite of the previous test percept, perceptual memory is reset. Accordingly, when the 'test' stimuli return the content of the memory has changed, or at least has been disrupted, hence perceptual stability is reduced. So perceptual memory is strongest for the most recent presentation, in this case the most recent presentation is the last interrupting stimulus.

In our second experiment, we investigated whether the perceptual memory which stabilises BR and SR is disrupted by non-rivalrous percepts. This experiment was the same as the first except that the latter 500 ms of the interrupting stimulus was non-rivalrous. Fig. 1d and e illustrates the sequence for the non-rivalrous interrupting stimuli for BR and SR, respectively. The perceptual sequence here simulates flash suppression.

The results (BR: Fig. 2c; SR: Fig. 2d), showed that when subjects were exposed to a non-rivalrous stimulus *opposite* in colour and orientation to that which they had *previously* experienced, perception remained stable across that interruption (Fig. 2c and d right columns). However, when the non-rivalrous interrupting stimulus was the *same* in colour and orientation as the previous rivalrous percept, perceptual stability was disrupted (Fig. 2c and d; left columns). The effect of the interrupting stimulus (same or different) was highly significant for BR ($P = 0.001$) and SR ($P < 0.001$), with a significant effect of subjects in the BR ($P = 0.03$) and in the SR condition ($P = 0.01$), although all subjects displayed qualitatively the same pattern of results.

What is perhaps most striking about the results of Experiments 1 and 2 is that the *perceptual* sequence each subject experienced was the same for each experiment. If for example during a 'same' condition a subject signalled a red percept, then perception during the interruption consisted of 500 ms of a green grating followed by 500 ms of a red grating (due to flash suppression in Experiment 1 or flash suppression simulation in Experiment 2). For the 'opposite' condition the interrupting sequence was the reverse. The two conditions affected perceptual stability quite differently. Interruptions consisting of the 'same' grating upheld stability when they were rivalrous, yet disrupted it when they were non-rivalrous. While the 'opposite' conditions disrupted stability when they were rivalrous and upheld stability when non-rivalrous. Hence the pattern of results in experiment two is the *inverse* of those in experiment one.

In addition to testing the effect of non-rivalrous and rivalrous gratings on BR and SR, we ran a third experiment which investigated the effect on perception when SR interrupted BR and vice versa. Fig. 3a and b shows data demonstrating that either type of rivalry disrupts the other in much the same way. During BR, test rivalry stability could be reduced by the presentation of a SR interruption stimulus and vice versa. The reduction in stability was largest when the dominant percept during the interrupting rivalry was *opposite* to that previously perceived during the test rivalry (Fig. 3a and b; right

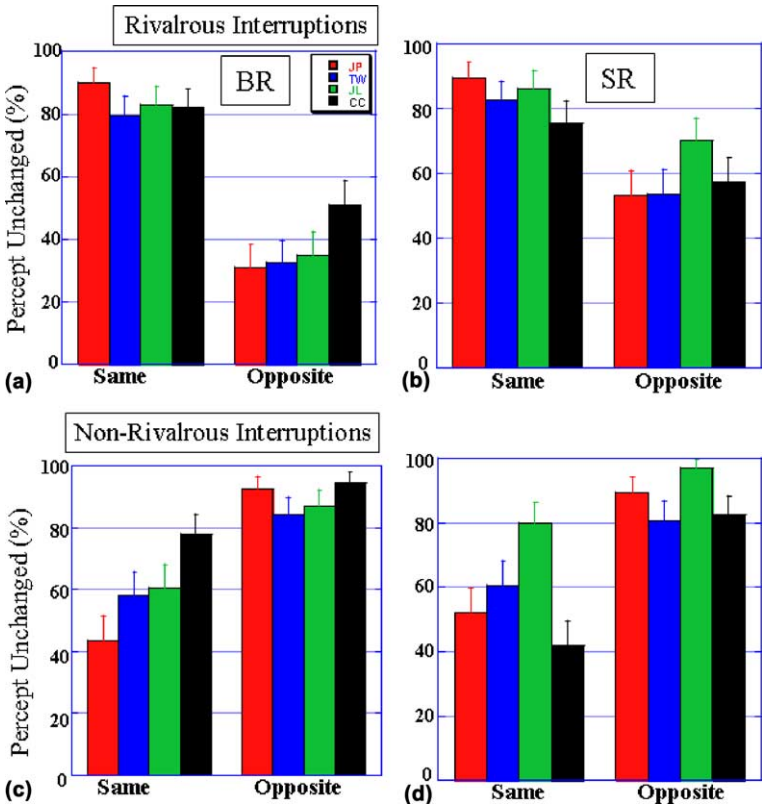


Fig. 2. Graphical illustration of the data from Experiments 1 and 2. The pattern of data in (a) and (b) is the inverse of that in (c) and (d). (a) BR used to interrupt tests stimuli of BR: left column depicts data from trials in which the percept consisted of the same features and sourced from the same eye for the latter 500 ms, as the dominant grating in the previous rivalry. The right column depicts data from trials in which the percept and eye were the opposite for the latter 500 ms of that previously dominant during rivalry. (b) SR used to interrupt test stimuli of SR: the left column depicts data from trials in which the latter percept was the same as that in the test rivalry. The right column depicts data from trials with the opposite percept to the previous test rivalry. (c) Test stimuli of BR interrupted by non-rivalrous monocular gratings. Left column depicts the percent stable of test stimuli across interruptions of non-rivalrous monoptic stimuli simulating flash suppression. The latter 500 ms consist of the same percept that was signalled during the previous rivalrous test presentation, the whole sequence is presented to the one eye. Right column: the opposite eye and percept to that previously signalled during test rivalry. Left column: is the same eye/grating. (d) Stability across test stimuli undergoing SR, when interrupted by binocular non-rivalrous stimuli. Left column depicts the same percept to that signalled during the previous test rivalry, the right depicts the opposite (in colour and orientation). Error bars on all graphs show 95% confidence intervals assuming binomial distribution of responses. The rightmost column in Fig. 3c and d shows the control data, stability with non-interruptions. (For interpretation of the references in colour in this figure, the reader is referred to the web version of this article.)

columns) but stability remained high when the *same* percept was presented (Fig. 3a and b; left columns). When SR was interrupting BR, the effect of the interrupting percept (same/opposite) was highly significant ($P = 0.003$) in the same direction as BR–BR. There were again significant inter-subject differences ($P = 0.032$), though all four subjects showed the same qualitative effect of lower stability across *opposite* interruptions. When BR was utilised to disturb SR the effect was highly significant ($P = 0.001$) in the same direction as SR–SR, with no significant subject effect ($P = 0.7$). In other words, the pattern of results here was the same as for those when the test and interrupting displays consisted of the same type of rivalry (BR–BR or SR–SR). These results suggest that the stabilising or priming effect found in Experiment 1 (rivalrous interrupting stimulus) is common across qualitatively different types of visual rivalry.

When up to three *different* bistable figures undergo interleaved intermittent presentation, perception is stabilised as with a single figure (Maier, Wilke, Logothetis, & Leopold, 2003). However, in that study perceptual changes were never 'forced'. We reasoned that rivalrous stimuli with different attributes (colour/orientation) might disrupt each other to a lesser extent than stimuli with common attributes. To investigate the effects of rivalrous stimuli with different attributes, we ran a fourth experiment in which the interrupting gratings were different to the test gratings in colour, orientation or both. Here the *interrupting* stimulus was always 'opposite' in whatever attributes it shared with the test stimulus and, during BR (interuption), the dominant grating was sourced from the opposite eye to that dominating during the preceding test phase. For example when the interrupting gratings consisted of ±45 orientation (the same as the test gratings), the opposite orienta-

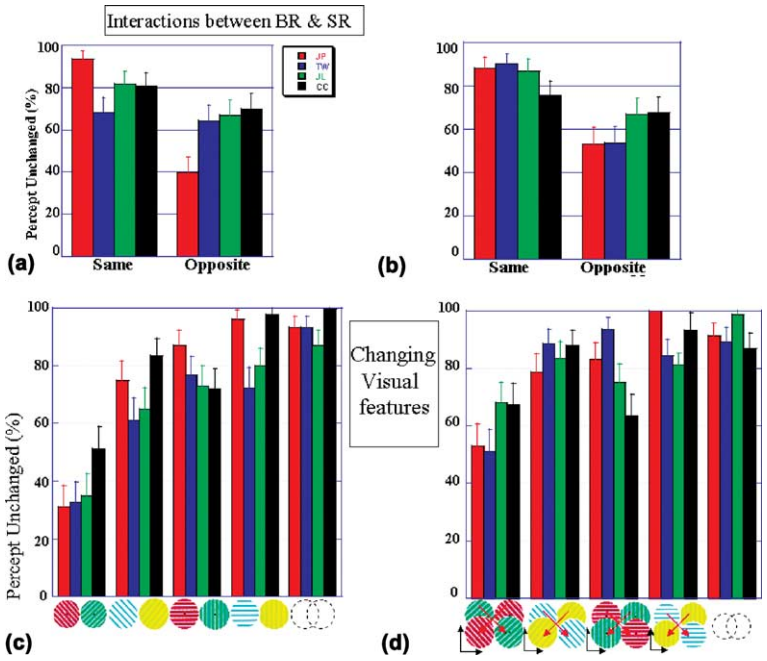


Fig. 3. Data from the interaction between BR and SR (Experiment 3) and the interrupting effect of gratings with different visual features. (a) Data from trials when opposite and same percept during SR interrupted test stimuli of BR (BR–SR). (b) Data from trials in which opposite and the same percept in BR interrupted test stimuli of SR (SR–BR). The pattern of data here is the same as that when the same type of rivalry disrupts stable perception of itself. (c) Test and disturb consisting of BR, test gratings: ±45 red/green. The type of disturb is depicted along the *x*-axis. The leftmost column depicts the 'opposite' data from Experiment 1, when attributes in the test and interruption are both the same. The rightmost column depicts data when the interruption is blank, the baseline data. The central three columns show data from interruptions with differing visual attributes. When either colour or orientation is changed perception is more stable than when attributes are the same. (d) When the test and disturb both consist of SR, test gratings: ±45 red/green. The graphics along the *x*-axis show the attributes used to interrupt stability. As with BR the stability is higher when the test and interruption do not share visual features. (For interpretation of the references in colour in this figure, the reader is referred to the web version of this article.)

tion was 'forced' during the interruption. All other aspects of this experiment were the same as those in Experiment 1. The results from the fourth experiment (Fig. 3c and d), show that changing either the colour, orientation or both of the interrupting gratings reduces the ability of those gratings to disrupt intermittent rivalry. For the colour condition the rivalrous interrupting stimulus consisted of ±45° yellow/purple gratings, in the orientation condition the stimuli consisted of vertical/horizontal red/green rivalrous gratings, and the condition in which both colour and orientation were different to those in the test rivalry consisted of yellow/purple-vertical/horizontal gratings. For these conditions the 'test' rivalry gratings were the same as those in all other experiments: ±45° red/green. The leftmost column of Fig. 3c and d illustrates the percentage of perceptual stability when the interrupting stimuli share both orientation and colour with the test stimuli (reproduction of the 'opposite' data from Experiment 1). The rightmost column confirms that perceptual stability is high with no interrupting presentation, only the 3 s blank gap: the baseline data (BR & SR).

The column second from the right depicts the percentage of trials in which perception was stable with an interrupting stimulus of different colours and orientations. A repeated-measurements ANOVA shows that there is no statistical difference in the percentage of trials stable between a blank interruption and a rivalrous stimulus with different attributes (BR: $P = 0.139$; SR: $P = 0.092$). The remaining two columns show the percentage of trials which remained stable when either the colour or orientation was changed independently. It would seem that, in order for rivalrous gratings to disturb perceptual memory, the interrupting gratings must share stimulus features with those in memory. The greater effect of interrupting stimuli sharing both colour and orientation with the test stimuli over those sharing just one attribute suggests a synergistic relationship between colour and orientation in perceptual memory rather than independent storage of the two attributes.

## 4. Discussion

Our results indicate that similar percepts in non-rivalrous and rivalrous vision have opposite effects on subsequent rivalrous vision. Rivalrous vision primes while non-rivalrous vision habituates. Both forms of rivalry we tested (BR and SR) had similar effects on subsequent rivalrous vision of either type. Rivalrous stimuli must

share common attributes to significantly disrupt this perceptual memory. When rivalry is presented intermittently perception stabilises (Leopold et al., 2002; Pearson & Clifford, 2004). Low-level neuronal adaptation might explain the interrupting effects of the non-rivalrous stimuli. However, it cannot account for the priming like effects of rivalrous stimuli.

Taken together, the current findings suggest that visual rivalry might recruit mechanisms that are not engaged in non-rivalrous vision. In fact it has been shown that ambiguous figures can influence one another, yet are not significantly influenced by the non-ambiguous version of the same figure (Grossmann & Dobbins, 2003). These behavioural findings complement existing brain imaging data demonstrating that parietal and prefrontal cortical areas are involved in rivalrous but not in non-rivalrous vision (Lumer & Rees, 1999; Lumer et al., 1998) and neuropsychological data demonstrating that right lateralized frontal brain damage can prevent perceptual reversals when viewing bistable figures (Meenan & Miller, 1994; Ricci & Blundo, 1990). On the basis that awareness during intermittent and continuous rivalry is determined by the same attributes of the visual stimulus (Chen & He, 2004; Pearson & Clifford, 2004), the current findings are presumed applicable to continuously viewed rivalry.

When an *unambiguous* figure is viewed for a long period, subsequent perception of an *ambiguous* figure is typically biased to be opposite that of the preceding unambiguous stimulus (Long, Toppinno, & Modin, 1992; Nawrot & Blake, 1989). However, when pre-presentation is brief (1 s), unambiguous patterns have been reported to prime subsequent ambiguous patterns (Long et al., 1992), such that the state of the ambiguous pattern is perceived to be the same as the unambiguous one. This trend does not seem to extend to BR and SR. When an image is presented to one eye only for either a short or long duration, followed by a rivalrous image to the other eye, perception flips to the second image: flash suppression (Wolfe, 1984). Similarly, we find that when a non-rivalrous stimulus is presented between intermittent presentations of a rivalrous stimulus, the subsequent rivalrous stimulus tends to be perceived opposite to the preceding non-rivalrous one even though the non-rivalrous stimulus is only present for 500 ms.

Interrupting stimuli composed of different visual attributes to those in memory do not significantly disrupt perceptual stability of another rivalrous stimulus. When the interrupting and test stimuli have one visual attribute in common (colour or orientation) perceptual stability is reduced, yet reduction in stability is markedly greater when both attributes are common to both stimuli. This demonstrates that when the test and interrupter share common attributes, the interrupting stimulus can gain access to or disturb perceptual memory. This suggests that access to a particular engram is highly selective, such that in order to interrupt or reset the perceptual memory a stimulus must resemble that in memory. In addition, it has been shown that this memory can be interrupted by voluntary eye movements (Ross & Ma-Wyatt, 2004). Together these characteristics may have some interesting implications for research into memory, particularly in comparison with normal visual memory (Magnussen, 2000; Magnussen & Greenlee, 1999).

Computationally, the neural substrate of binocular rivalry is typically viewed as a competitive interaction between dynamic neuronal assemblies (Dayan, 1998; Lehky, 1988; Wilson, 2003). When competing assemblies are active, it is the interactions between them that resolve the competition; hence continuously viewed rivalry oscillates back and forth between two competing stimuli. Collectively, the strength and spread of these connections constitute a form of short-term perceptual memory (Hopfield, 1982). We propose that it is the state of the connections mediating these interactions that underlies perceptual stability during intermittent rivalry. When the stimuli are removed from vision during intermittent rivalry the state of the connections mediating the competition does not change. Moreover, because presentation times are brief during intermittent rivalry, the connections do not have sufficient time to change significantly during stimulus presentation.

When a non-rivalrous stimulus is presented during the interruption only one neuronal assembly is activated. That assembly is presumed to be adapted or fatigued, such that its responsiveness is reduced. When the rivalrous test stimuli return, competition will be biased against the stimulus sharing attributes with the non-rivalrous interrupting stimulus. Hence, a non-rivalrous interrupting stimulus that matches the percept reported in the previous test phase will tend to weaken the competitive strength of a similar stimulus presented during the subsequent test phase, causing a reduction in perceptual stability from one test phase to the next (similar to the technique of flash suppression; Wolfe, 1984).

When a rivalrous interrupting stimulus forces the dominant percept to be opposite to that reported in the previous test phase (flash suppression), this opposite percept tends to reconfigure the short-term perceptual memory, resulting in a reduction in stability of the previous test percept. While low-level adaptation presumably plays a part in generating flash suppression, once both gratings are present we propose that it is the interactions between them that reconfigure the state of the perceptual memory responsible for stable perception during intermittent rivalry. Low-level adaptation cannot explain perceptual stability during intermittent rivalry (Leopold et al., 2002; Maier et al., 2003; Pearson & Clifford, 2004). Instead, we propose that when flash suppression resets the dominant percept through a rivalrous interruption, it is the perceptual memory for

bistable stimuli which configures subsequent rivalry. This type of model can seemingly account for the opposite effects of rivalrous and non-rivalrous interrupting stimuli evident from the current data.

The current work suggests that a particular mechanism might be activated during rivalrous vision, yet not during non-rivalrous vision. If such mechanisms do exist where in the brain might they reside? Lumer and colleagues (Lumer et al., 1998) put forward a hypothesis as to why identical sequences of percepts in rivalrous and non-rivalrous conditions might involve different event-related activity. Because perceptual shifts during rivalry derive from endogenous neural instability, while during the non-rivalrous condition perception is contingent on changes in exogenous visual input, they suggest that the two processes might involve different brain areas. In this case, the difference in BOLD signal might reflect the activity of mechanisms underlying the resolution of visual conflict during rivalrous or bistable stimulation. If the two different types of visual awareness (rivalrous and non-rivalrous) do indeed involve different neural counterparts (at some level of processing) then one might expect a perceptual consequence, such as the one documented here, should follow.

It has been suggested that the range of functions associated with the parietal and prefrontal areas argues against the existence of a specialised mechanism for rivalry (Lumer & Rees, 1999). Instead, the conjunction of activity in these areas may form a more general mechanism which mediates the integration of internal representations of visual elements into the broader context of visual awareness.

Whether a specialised cortical mechanism exists for the resolution of visual conflict or a more general mechanism is applied to conflicting visual input, the two types of visual awareness (rivalrous and non-rivalrous) are dissociable. With evidence from the current psychophysical study, functional imaging (Kleinschmidt et al., 1998; Lumer & Rees, 1999; Lumer et al., 1998) and neuropsychology (Meenan & Miller, 1994; Ricci & Blundo, 1990) converging to support the existence of such a mechanism, further exploration is clearly warranted.

## 5. Conclusion

The current work demonstrates a possible perceptual consequence of the additional activity observed in parietal and prefrontal areas during rivalrous vision (Lumer & Rees, 1999; Lumer et al., 1998). Rivalrous and non-rivalrous stimuli affect subsequent rivalrous vision in different ways. This suggests that specific neural machinery might be engaged to resolve visual competition. This machinery demonstrates a synergistic relationship between different visual features and perhaps involves a network of extrastriate, parietal and prefrontal areas. These findings prompt new inquiry regarding a common underlying assumption: that the study of rivalrous awareness informs us about non-rivalrous awareness. We feel that current understanding could be greatly enhanced with the addition of single cell physiology and further imaging research investigating possible dissociations between different states of visual awareness. This line of research should in time help reveal the seemingly mysterious underpinnings of our visual world.

## Acknowledgments

This work was supported by a Queen Elizabeth II Fellowship and Discovery Project Grant awarded to CC by the Australian Research Council. We are grateful to Dr. Justin Harris and anonymous reviewers for thoughtful comments on earlier versions of this manuscript.

## References

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience, 3*, 1–11.

Chen, X., & He, S. (2004). Local factors determine the stabilization of monocular ambiguous and binocular rivalry stimuli. *Current Biology, 14*, 1013–1017.

Crick, F., & Koch, C. (1998). Consciousness and neuroscience. *Cerebral Cortex, 8*, 97–107.

Dayan, P. A. (1998). Hierarchical model of binocular rivalry. *Neural Computation, 10*, 1119–1135.

Engel, A. K., Fries, P., Konig, P., Brecht, M., & Singer, W. (1999). Temporal binding, binocular rivalry, and consciousness. *Consciousness and Cognition, 8*, 128–151.

Grossmann, J. K., & Dobbins, A. C. (2003). Differential ambiguity reduces grouping of metastable objects. *Vision Research, 43*, 359–369.

Hopfield, J. J. (1982). Neural networks and physical systems with emergent collective computational abilities. *Proceedings of the National Academy of Science USA, 79*, 2554–2558.

Kleinschmidt, A., Buchel, C., Zeki, S., & Frackowiak, R. S. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society of London Series B—Biological Sciences, 265*, 2427–2433.

Lee, S. H., & Blake, B. (1999). Rival ideas about binocular rivalry. *Vision Research, 39*, 1447–1454.

Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception, 17*, 215–228.

Leopold, D. A., Wilke, M., Maier, A., & Logothetis, N. K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience, 5*, 605–609.

Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society of London: B, 353*, 1801–1818.

Logothetis, N. K. (1999). Vision: A window on consciousness. *Scientific American, 281*, 69–75.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature, 380*, 621–624.

Long, G. M., Toppinno, T. C., & Modin, G. W. (1992). Prime time: Fatigure and set effects in the perception of reversible figures. *Perception and Psychophysics, 52*, 609–616.

Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science, 280*, 1930–1934.

Lumer, E. D., & Rees, G. (1999). Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proceedings of the National Academy of Science USA, 96*, 1669–1673.

Magnussen, S. (2000). Low-level memory processes in vision. *Trends in Neurosciences, 6*, 247–251.

Magnussen, S., & Greenlee, M. W. (1999). The psychophysics of perceptual memory. *Psychological Research, 62*, 81–92.

Maier, A., Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Perception of temporally interleaved ambiguous patterns. *Current Biology, 13*, 1076–1085.

Meenan, J. P., & Miller, L. A. (1994). Perceptual flexibility after frontal or temporal lobectomy. *Neuropsychologia, 32*, 1145–1149.

Nawrot, M., & Blake, R. (1989). Neural integration of information specifying structure from stereopsis and motion. *Science, 244*, 716–718.

Pearson, J., & Clifford, C. W. G. (2004). Determinants of visual awareness following interruptions during rivalry. *Journal of Vision, 4*, 196–202, URL: http://journalofvision.org/4/3/6/.

Ricci, C., & Blundo, C. (1990). Perception of ambiguous figures after focal brain lesions. *Neuropsychologia, 28*, 1163–1173.

Ross, J., & Ma-Wyatt, A. (2004). A. Saccades actively maintain perceptual continuity. *Nature Neuroscience, 7*, 65–69.

Wheatstone, C. (1838). On some remarkable and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London, 128*, 371–394.

Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron, 39*, 1043–1052.

Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences of the United States of America, 100*, 14499–14503.

Wolfe, J. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research, 24*, 471–478.